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FEEDING PREFERENCES OF TWO PREDATORY SNAILS INTRODUCED TO HAWAII AND THEIR CONSERVATION IMPLICATIONS

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ABSTRACT

Two introduced predatory land snails, *Euglandina rosea* and *Oxychilus alliarius*, have been implicated in the decline of native Hawaiian and Pacific island land snails. We examined the feeding ecology of *E. rosea* and *O. alliarius*, focusing first on prey size and species preferences, and second on quantifying consumption rates, which is necessary to address the possible levels of impact on natural populations. In prey-size preference experiments, *E. rosea* always consumed more snails in the smaller size class. In prey-species preference experiments, *E. rosea* preferred snails to slugs but showed no preference among snail species. Size preference experiments indicated that *O. alliarius* will only consume prey less than 3 mm in shell length. In prey species preference experiments *O. alliarius* consumed every snail species offered but did not consume either of the slug species. Consumption rates were positively related to the size of the predator, with the larger predator, *E. rosea*, having a much higher consumption rate than *O. alliarius*, and with larger *E. rosea* consuming more than smaller *E. rosea*. These results have unfortunate conservation ramifications, because since they indicate that both *E. rosea* and *O. alliarius* are generalist snail predators feeding preferentially on the smallest snails, although they rarely eat slugs. Since many extant Hawaiian and Pacific island snail species are small, they are at risk of predation by these two introduced predators, while invasive slugs – there are no native slugs in Hawaii – may not be impacted by them.

Key words: consumption rate, *Euglandina rosea*, Gastropoda, *Oxychilus alliarius*, slug.

INTRODUCTION

Land-snail faunas world-wide are under extreme threat, and have the dubious honor of having the highest number of documented extinctions of any major taxonomic group (Cowie, 2004; Nash, 2004; Lydeard et al., 2004). The 2008 *IUCN Red List of Threatened Species* (IUCN, 2008) included 1,994 gastropods (snails and slugs), of which 271 were listed as extinct. Native Pacific island land snails, in particular, are recognized for their diversity, high levels of endemism and the fact that they are under extreme threat, with perhaps as many as 50% of the species having disappeared (Lydeard et al., 2004). For example, extinction of the tree-snail species (Achatinellinae in Hawaii and Partulidae on other Pacific islands) has been catastrophic (Clarke et al., 1984; Hadfield, 1986; Murray et al., 1988; Cowie, 1992; Hadfield et al., 1993; Coote & Loève, 2003).

In Hawaii, the situation may be especially critical. The native Hawaiian land-snail fauna used to be extremely diverse (over 750 species) and exhibited extremely high endemism (over 99%) (Cowie et al., 1995), but estimates of extinction of these unique species range from 65–75% (Solem, 1990) to 90% (Cowie, 2002; Lydeard et al., 2004). For example, the Amastridae, an endemic Hawaiian family of more than 300 species (Cowie et al., 1995), may now be reduced to as few as ten or so species existing in tiny, highly localized, remnant populations. The Endodontidae in Hawaii and throughout the Pacific appear reduced to sparse populations on those islands they formerly inhabited (Lydeard et al., 2004; Meyer, 2006).

Two introduced predatory land snails, *Euglandina rosea* and *Oxychilus alliarius*, have been implicated in the decline of the native land-snail faunas. *Euglandina rosea* was purposely introduced to Hawaii in 1955 to control populations

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of another introduced snail, *Achatina fulica*, the giant African snail (Davis & Butler, 1964; Simberloff, 1995; Civeyrel & Simberloff, 1996; Cowie, 2001). Subsequently, it was introduced elsewhere (Mead, 1961) and is now widely distributed throughout the Pacific (Cowie, 2001; Cowie et al., 2008). Unfortunately, the introduction of *E. rosea* has not reduced *A. fulica* populations (Civeyrel & Simberloff, 1996; Cowie, 2001), but has been associated with the decline of many of the tree-snail species, not only in Hawaii but elsewhere in the Pacific (Clarke et al., 1984; Hadfield, 1986; Hadfield et al., 1993; Murray, 1993; Gerlach, 2001; Coote & Loève, 2003), and may have caused the extinction of other native land-snail species (Cowie, 1998, 2001). Native to Europe, *O. alliarius* was first recorded in the Hawaiian Islands in 1937 (Cowie, 1997). Ignored until more recently, *O. alliarius* has become extremely abundant on the islands of Maui (Severns, 1984) and Hawaii (Meyer & Cowie, in press) and now occurs also on Molokai and Kauai (Cowie, 1997) and on Oahu (W. M. M., personal observation). *Oxychilus alliarius* is omnivorous, but is known as a snail predator; it may have played a role in the decline of the native Hawaiian land snail fauna, as it is thought to have done in New Zealand (Barker & Efford, 2004), and it could be a threat to the remaining extant species (Severns, 1984).

Certain aspects of the feeding ecology of *E. rosea* have been studied, including feeding behavior and prey trail following (Cook, 1985a, b; Gerlach, 1999), prey-size preferences (Chiu & Chou, 1962; Davis & Butler, 1964; Nishida & Napompeth, 1975; Cook, 1989a, b; Gerlach, 1999), and prey-species selection in the wild (Griffiths et al., 1993). However, extrapolating from these results to determine the effect *E. rosea* is having on land snail faunas as a whole is difficult, especially because consumption rates and the reasons for prey preferences have not been adequately addressed. For instance, experiments that addressed species preferences did not control for prey size among prey species offered (Cook, 1989a, b). Instead, total weight of each species was standardized. However, if prey size is as important as suggested (Chiu & Chou, 1962; Davis & Butler, 1964; Nishida & Napompeth, 1975; Cook, 1989a, b), the fact that the smaller species were preferred in choice experiments tells us little about preferences for specific species. Also, the microcosms used in these experiments (clear glass dishes) did not provide conditions permitting all possible predator avoidance behaviors. We know of no reports of feeding preference experiments on *O. alliarius*.

Despite the two predators' reputations, relatively little attention has been paid to the biology of either. Our objective was to examine the feeding ecology of *E. rosea* and *O. alliarius*, focusing first on prey-size and species preferences, and second on quantifying consumption rates in order to address the possible levels of impact on natural populations.

METHODS

All experiments were conducted with snails collected from the wild less than one month previously. They were allowed to acclimate to laboratory conditions for at least three days prior to any experiments. Both predator species were fed a diet of *Bradybaena similaris*, a common invasive snail in Hawaii. *Bradybaena similaris* was not used as a prey species in the subsequent experiments. All animals were maintained in the same kind of containers as those used in the experiments: 30 x 20 x 30 cm for *E. rosea*; 5 x 5 x 5 cm for *O. alliarius*. Laboratory temperatures were 19–24°C during the experiments.

Different methods were used to assess the feeding behavior of each predator, since *E. rosea* has a much higher consumption rate than *O. alliarius*. The primary difference between the methods were that experiments examining *E. rosea* preferences (prey size and species) were choice experiments, with individual predators given a choice between two prey options, while *O. alliarius* experiments were no-choice, as each predator was only offered one prey option. A different individual was used as a predator for every replicate across all experiments. For the *E. rosea* experiments, because hundreds of prey individuals were required, we used only non-native species, from five distinct families: two slug species (*Veronicella cubensis*, *Deroceras laeve*) and three snail species (*Achatina fulica*, *Paropeas achatinaceum*, *Succinea tenella*). These species are phylogenetically diverse, such that the results should be generalisable. Inclusion of a species of non-native Succineidae, a family that has proportionately more extant native species in Hawaii than any other family (Rundell et al., 2004), also provides more specific relevance to the local fauna. Given the much lower consumption rates of *O. alliarius*, it was reasonable to include native species as prey (*Succinea* spp., *Philonesia* sp., *Tornatellides* spp.) in addition to common invasive species (*Arion intermedius*, *Deroceras laeve*, *Paropeas achatinaceum*), all of which occur in areas in Hawaii with abundant *O. alliarius*.

Prey-Size Preference

Euglandina rosea

Seventeen adult *E. rosea* (35–55 mm shell length) were starved for two days prior to experimentation to standardize hunger levels. Each experimental container was filled with 2 cm of soil, a calcium source (cuttle bone), and some lettuce leaves as food for the prey. The prey (*A. fulica*) were divided into four size classes (0–1, 1–2, 2–3, and 3–4 cm shell length). Ten snails from two of the four size classes were offered to one *E. rosea* after the prey had been allowed to acclimate to the container for one day. *Euglandina rosea* consumes small snails whole as well as eating larger snails via the shell aperture. Every 12 h consumed individuals were replaced with new individuals of the same size class. No more than four snails of one size class were replaced at one interval, so a choice of prey was always available. Experiments were run for four to ten days depending on consumption rates and prey availability. At the end of the experiments, the numbers of small prey and large prey consumed were added up for each container. Differences in preference between small and large prey were assessed by comparing the number of containers with more small prey consumed to containers with more large prey consumed using a sign test (Sokal & Rohlf, 1995).

Oxychilus alliarius

Adult *O. alliarius* (6–10 mm shell width) were offered prey (native *Succinea* spp. from areas where *O. alliarius* is abundant) of various sizes. One prey item was placed in a container with 2 cm of soil and one leaf of *Broussaisia arguta* to provide it with habitat and food. Prey were divided into six size classes (1–3, 3–5, 5–7, 7–9, 9–11, and 11–13 mm shell length). Seventy-four experimental replicates each contained one adult *O. alliarius* in addition to the prey snail, while 48 control replicates each contained only the prey snail. Each trial was run for seven days at the end of which prey were recorded as alive or dead. We have only seen *O. alliarius* feed via the aperture, as opposed to consuming the entire prey snail including its shell. Differences in mortality between control and experimental treatments for each size class were tested using the log odds ratio, $l(o)$ (Sokal & Rohlf, 1995), as follows:

$$l(o) = \ln\left[\frac{((N_{11} + 0.5) / (N_{12} + 0.5))}{((N_{21} + 0.5) / (N_{22} + 0.5))}\right]$$

which is useful because it permits standard errors, $s_{l(o)}$, to be calculated from binary data, as follows:

$$s_{l(o)} = \left(\frac{1}{(N_{11} + 0.5)} + \frac{1}{(N_{21} + 0.5)} + \frac{1}{(N_{12} + 0.5)} + \frac{1}{(N_{22} + 0.5)}\right)^{1/2}$$

where N_{11} is the number of experimental replicates in which the prey survived; N_{12} is the number of control replicates in which the species survived; N_{21} is the number of experimental replicates in which the prey died; N_{22} is the number of control replicates in which the prey died.

If mortality is equal in control and experimental treatments the log odds ratio is zero. Significant differences in mortality were determined when a log odds ratio was: 1) further than 1.96 standard errors away from zero ($p < 0.05$), and 2) further than 2.576 standard errors away from zero ($p < 0.01$).

Prey-Species Preference

Euglandina rosea

Prey-species preference of *E. rosea* was assessed by offering a choice between two of the five prey species listed above. Prey were 5–15 mm in extended foot length. The size distribution, that is, the numbers of snails/slugs of various sizes in each trial, was matched between the two prey species in order to minimize any effect of size in determining species preference. Using the length of the extended foot, rather than a shell size measure, was necessary since some of the prey choices were slugs (*V. cubensis* and *D. laeve*). Of the ten possible pair-wise combinations, eight were tested (*D. laeve* vs. *S. tenella* and *D. laeve* vs. *A. fulica* were excluded because of lack of adequate numbers of *D. laeve*). There were ten replicates for each pair-wise combination. A different *E. rosea* and 20 prey (ten individuals of two species) were used in each replicate. The number of each type of prey consumed (no replacement) over a 24 h period was recorded.

A preference index was calculated for each predator in each replicate/container using a version of Manly's α index that accounts for variable prey populations, that is where prey are not replaced (Krebs, 1999), as follows:

$$\alpha_i = \frac{\mathrm{Log}\ p_i}{\sum_{i=1}^{m} p_j}$$

where α_i is Manly's α (preference index) for prey type i; p_i, and p_j are the proportions of prey i or j remaining at the end of the experiment (i = 1, 2, 3, … m; j = 1, 2, 3, … m), that is, e_i/n_i in which e_i is the number of prey type i remaining uneaten at the end of the experiment, n_i is the initial number of prey type i in the experiment, and m is the number of prey types (similarly for e_j/n_j). Values for this index range between 0 and 1; values > 0.5 indicate preference and values < 0.5 avoidance. Significance of divergence from 0.5 (no preference) was assessed with single sample t-tests.

Oxychilus alliarius

Prey-species preference of *O. alliarius* was assessed by offering adults (6–10 mm maximum shell width) a single prey individual of various species (< 3 mm maximum shell dimension for snails and similarly sized slugs determined by matching foot size between slugs and snails) following the same procedure and analyses as in the *O. alliarius* prey-size experiments. Prey species used were: the native snail species *Succinea* spp. (33 experimental trials, 18 controls), *Tornatellides* spp. (13,15), and *Philonesia* sp. (12,12); the invasive snail species *P. achatinaceum* (10,8); and the invasive slug species *A. intermedius* (17,17) and *D. leave* (11,10).

Consumption Rate

Euglandina rosea

Twelve *E. rosea* were used in consumption rate experiments (seven adults 40–55 mm shell length, five juveniles 10–25 mm shell length). For a week prior to the experiments, they were provided with prey snails (*A.fulica*, *P. achatinaceum*, *B. similaris*) of various sizes *ad libitum*. Snails were not starved, so that the consumption rate measured would be a more natural rather than a maximum rate. Thirty prey snails (non-native *Succinea tenella*, 15 in the size range 1–5 mm and 15 in the range 5–12 mm shell length) were then offered to an individual *E. rosea* for a period of 24 h. Each prey snail was weighed to the nearest 0.0001 g and individually marked. At the end of the experiment, the number of snails remaining alive was counted, and any shells remaining from consumed snails were weighed to the nearest 0.0001 g, these weights being subtracted from the weights of those snails at the beginning of the experiment to give a value of the weight consumed. Adding this amount to the known weight of snails consumed whole provided a value for the total weight consumed. Growth of prey snails over the 24 h of the experiment was assumed to be negligible. Wet weight consumed was regressed on *E. rosea* size. Manly's α index (described above) was used to define preference, followed by a Mann-Whitney U-test to test for significant differences in preference for small prey (1–5 mm) vs. large prey (5–12 mm) between adult and juvenile *E. rosea*.

TABLE 1. Number of *Achatina fulica* eaten by *Euglandina rosea* when given a choice between two size classes. Each experiment used a different *E. rosea* individual.

		Number Eaten	
Size Classes	Duration (days)	Smaller	Larger
0–1 vs. 1–2 cm	4	10	2
	4	9	0
	4	13	0
	4	2	0
0–1 vs. 2–3 cm	5	11	0
	5	4	0
0–1 vs. 3–4 cm	5	10	0
1–2 vs. 2–3 cm	5	4	0
	5	4	0
	5	3	0
	5	0	0
1–2 vs. 3–4 cm	4	3	0
	4	1	0
2–3 vs. 3–4 cm	10	0	0
	10	2	0
	10	1	0
	10	0	0
Total		77	2

TABLE 2. Predation of *Oxychilus alliarius* on native *Succinea* spp. of different size classes (shell length). P-Value based on log odds ratio tests. NS indicates P-Values > 0.05.

	Control		Experimental		
Size Class	No. Survived	No. Died	No. Survived	No. Died	P-value
0–3 mm	20	0	3	33	< 0.01
3–6 mm	16	0	16	0	NS
6–9 mm	17	0	17	0	NS
> 9 mm	12	1	12	0	NS

Oxychilus alliarius

Twelve *O. alliarius* were used in consumption-rate experiments. They were collected from the field and placed directly into individual containers each with five prey snails (*Succinea* spp., 1–3 mm shell length) for seven days. Each prey item was weighed to the nearest 0.0001 g and was individually marked prior to being placed in the container. At the end of the experiment, the snails remaining alive were counted and any shells remaining from consumed snails were weighed to the nearest 0.0001 g, these weights being subtracted from the weights of those snails at the beginning of the experiment to give a value of the weight consumed.

RESULTS

Prey-Size Preference

Regardless of which snail combination *E. rosea* was offered (Table 1), in all cases in which at least one prey was consumed (14 of 17) more of the smaller snails were consumed (sign test: $P < 0.001$). Even being extremely conservative and considering the three instances in which no prey were eaten and the one in which two of the larger prey were eaten (in the 0–1 vs. 1–2 cm trials) as supporting the null hypothesis of no preference, gives a two-sided P-Value of 0.049. Pooling the data, 77 snails in the smaller size class were consumed

TABLE 3. Results of pair-wise comparison of preferences (Manly's α) of *E. rosea* among five prey species: *Vc = Veronicella cubensis*, *Dl = Deroceras laeve* (the two slug species), *Pa = Paropeas achatinaceum*, *Af = Achatina fulica*, *St = Succinea tenella*. Values of α > 0.5 indicate preference; Values < 0.5 indicate avoidance. A single sample t-test was used to test if the preference indices differed significantly from 0.5. Statistically significant differences are indicated by asterisks (P-values are < 0.01 in all cases).

Treatment	Manly's α Preference Index (SE)	
Snails vs. Snails		
Pa vs. *St*	*Pa* = 0.417 (0.221)	*S* = 0.583 (0.211)
Pa vs. *Af*	*Pa* = 0.482 (0.255)	*Af* = 0.518 (0.255)
Af vs. *St*	*Af* = 0.459 (0.151)	*S* = 0.541 (0.151)
Slugs vs. Snails		
Vc vs. *Pa*	*Vc* = 0.039 (0.089)*	*Pa* = 0.961 (0.089)*
Vc vs. *St*	*Vc* = 0.009 (0.024)*	*S* = 0.991 (0.024)*
Vc vs. *Af*	*Vc* = 0.029 (0.086)*	*Af* = 0.971 (0.086)*
Dl vs. *Pa*	*Dl* = 0.137 (0.082)*	*Pa* = 0.863 (0.082)*
Slugs vs. Slugs		
Dl vs. *Vc*	*Dl* = 0.893 (0.168)*	*Vc* = 0.106 (0.168)*

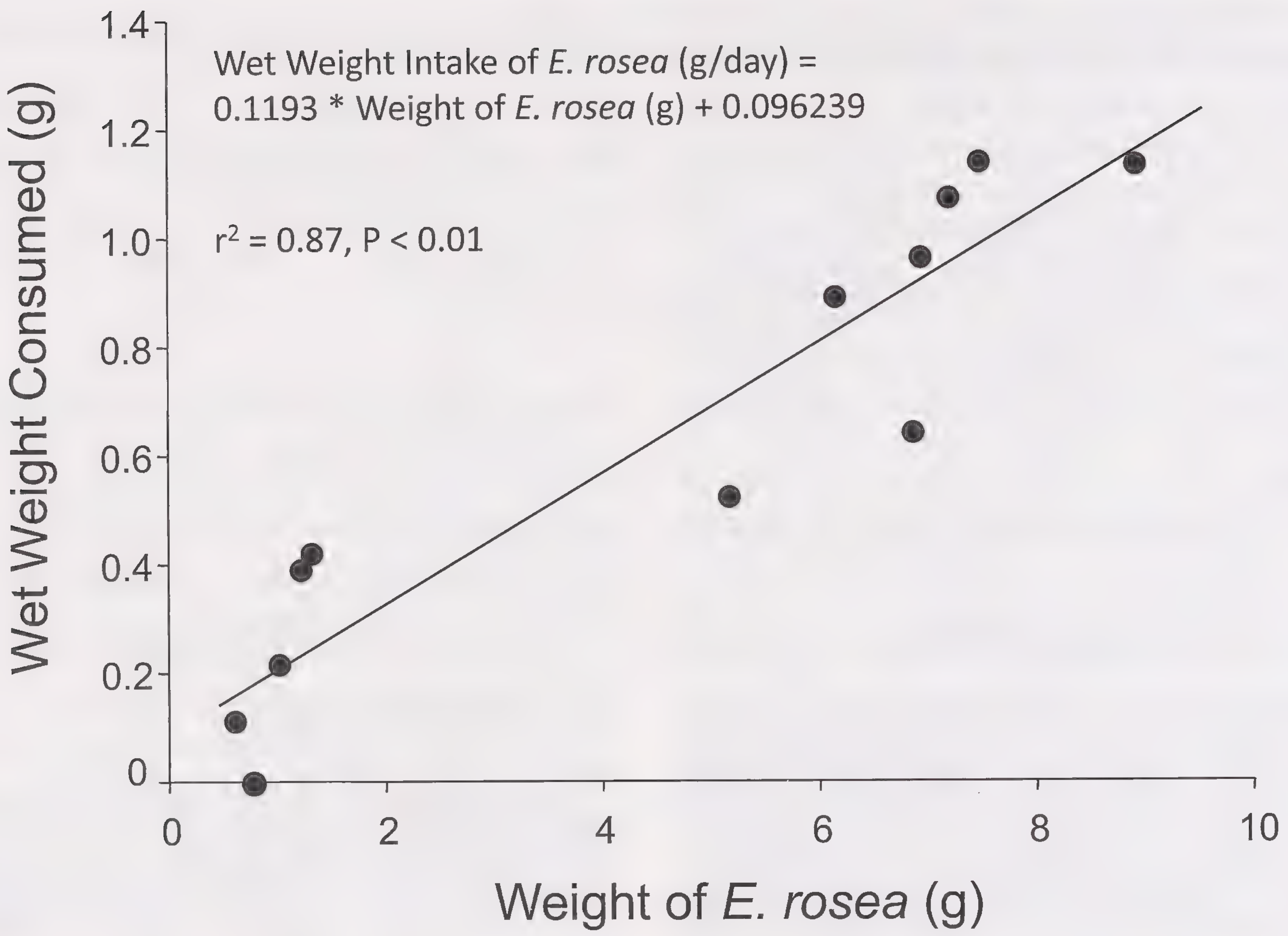

FIG. 1. Consumption rate (wet weight consumed during a 24 h period) vs. weight of *Euglandina rosea*.

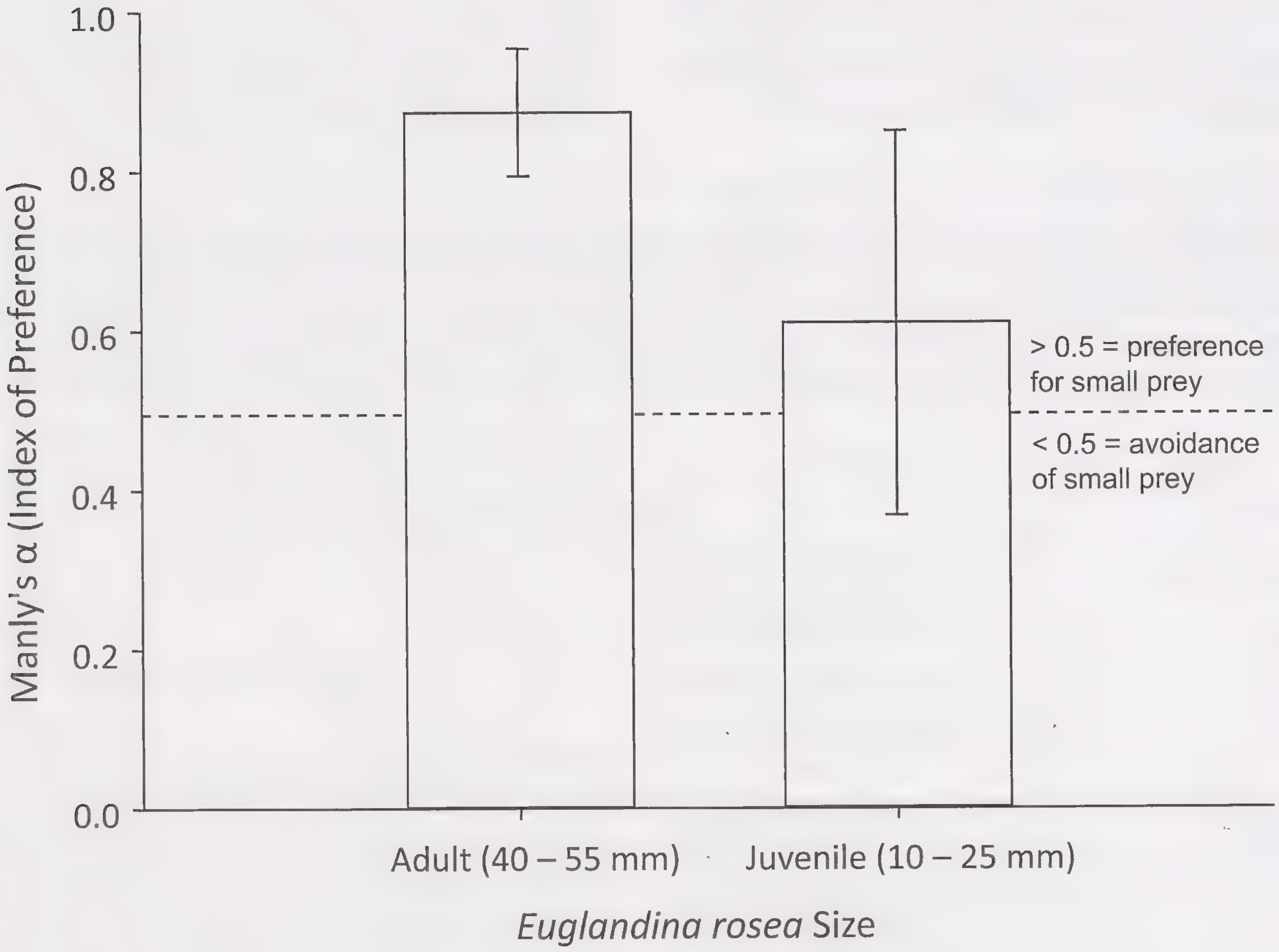

FIG. 2. Manly's α indices for adult and juvenile *E. rosea* preference for smaller prey (1–5 mm shell length) or larger prey (5–12 mm shell length). Error bars represent ± 1 standard error.

TABLE 4. Predation of *Oxychilus alliarius* on native and introduced snails (*Succinea* spp., *Tornatellides* spp., *Philonesia* sp., *P. achatinaceum*) and slugs (*D. laeve* and *A. intermedius*). P-Value based on log odds ratio tests. NS indicates P-values > 0.05. *Native species.

	Control		Experimental		
Taxa	No. Survived	No. Died	No. Survived	No. Died	P-value
Snails					
Succinea spp.*	18	0	6	25	< 0.01
Tornatellides spp.*	14	1	1	12	< 0.01
Philonesia sp.*	12	0	4	8	< 0.05
P. achatinaceum	8	0	1	9	< 0.05
Slugs					
D. laeve	10	0	10	1	NS
A. intermedius	16	1	17	0	NS

compared to only two from the larger size class. *Euglandina rosea* thus prefers smaller snails when given a choice.

In the *O. alliarius* experiments, no snail above 3 mm in shell length was preyed upon compared to 33 of the 36 (91%) that were 3 mm in shell length or less; hence, there was no significant difference between control and experimental treatments except in the 0–3 mm prey size category (Table 2).

Prey-Species Preference

Euglandina rosea always preferred the snail over the slug species but showed no preference among the three snail species (Table 3). *Veronicella cubensis* was the least preferred prey, and *D. laeve* seemed to be preferred over *V. cubensis* but was less attractive than *P. achatinaceum* and therefore probably also less attractive than the other snail species (*S. tenella* and *A. fulica*).

Oxychilus alliarius readily consumed all snail species offered, as indicated by the much higher mortality in the experimental treatments, but there was no difference in mortality between control and experimental treatments for the two slug species (Table 4).

Consumption Rate

Wet weight consumed increased as *E. rosea* weight increased (Fig. 1). The high r^2 value (Fig. 1) suggests that this mathematical model describes the relationship well. The regression line was not forced to go through the origin but the y-intercept was nevertheless close to it. Adult *E. rosea* preferred smaller snails to larger snails ($\alpha = 0.874$, SE = 0.080; T =12.35, df = 6, $P < 0.001$), but juvenile *E. rosea* showed no preference ($\alpha = 0.609$, SE = 0.241; T = 0.905, df = 3, P = 0.432). The difference in preference was significant (U = 26.0, P = 0.023; Fig. 2).

The consumption rate for *O. alliarius* was 0.00097 (± 0.00019 SE) g of wet weight per day, which equates to about one snail (1–3 mm maximum shell dimension) consumed by each individual during the experiment (7 days).

DISCUSSION

Small snails were more vulnerable to predation by both *E. rosea* and *O. alliarius*. While *O. alliarius* can only consume small snails (less than 3 mm maximum shell dimension), *E. rosea* can consume larger prey. However, when given a choice of prey sizes, *E. rosea* will eat significantly more small snails than large snails (Table 1, Fig. 2). These results are consistent with other studies of prey size preference in *E. rosea* (Chiu & Chou, 1962; Davis & Butler, 1964; Nishida & Napompeth, 1975; Cook, 1989a, b; Griffiths et al., 1993; Gerlach, 1999). However, our results indicate that this size preference is relative not absolute, that is, mid-sized prey (1–2 or 2–3 cm in shell length) are not eaten if presented along with smaller prey, but are eaten if presented with larger prey (Table 1). It is not simply that larger prey cannot be eaten. This behavioral flexibility is interesting, and perhaps important for the dynamics of the interaction, although the data are too few to evaluate further. Nonetheless, our results and those of other studies indicate that differences in size among prey can influence the predatory behavior of *E. rosea*, and thus confound conclusions of prey species preference if prey size is not appropriately controlled in experiments.

The size of *E. rosea* is also important in understanding prey-size preference. Although counter-intuitive, larger *E. rosea* had a stronger preference for smaller prey (Fig. 2). This may be because large *E. rosea* have a greater ability to consume snails whole. Thus, the impact of large *E. rosea* on small snails may be even greater. In the field, a large majority of the species consumed by *E. rosea* were swallowed whole (Griffiths et al., 1993). One reason usually proposed for *E. rosea*'s preference for smaller snails is calcium intake. Cook (1989a) suggested that there may be a compromise between the input of important nutrients, primarily calcium, when the prey is consumed whole (shell included), and the caloric intake that comes from the consumption of just body tissue.

Both predators exhibited a clear preference for the snail species over the slug species in all tests (Tables 3, 4). In all experiments examining *E. rosea*'s preference between snails and slugs, it preferred the snails, while showing no preference among snail species in snail vs. snail experiments (Table 3). However, between the slugs, *E. rosea* did prefer *D. laeve* over *V. cubensis* (Table 3). *Oxychillus alliarius* showed similar preferences, consuming all snail species offered but no slugs (Table 4). There are no native slugs in Hawaii, but non-native slugs are abundant and widespread (Cowie et al., 2008; Meyer & Cowie, in press) and negatively influence Hawaiian ecosystems by reducing survivorship of young native plants (Joe & Daehler, 2008). Thus, predation on slugs could *a priori* be seen as a positive counter balance to the introduction of these predatory snails, but unfortunately, our results show that both *O. alliarius* and *E. rosea* prefer snails to slugs, and many of the slugs reach sizes well above the preferred size range of both *O. alliarius* and *E. rosea*.

Consumption rate was related to predator size. That of *O. alliarus* was much lower than that of *E. rosea*, reflecting the much smaller size of *O. alliarius*; and within *E. rosea* consumption rate increased with predator size (Fig. 1). However, the impact of *O. alliarius* on native snails may still be considerable because of the high densities this species can reach, notably at higher elevations on the islands of Maui and Hawaii.

Many of the extant native Pacific Island snails are small (e.g., numerous endodontids, helicinids, vertiginids, and achatinellids (excluding Achatinellinae) are < 3 mm in maximum shell dimension for their entire life) compared to some of the abundant introduced snails/slugs that have become established (e.g., *Achatina fulica*, *Cornu aspersum*, *Limax maximus*, *Veronicella cubensis*, and *Meghimatium striatum*) (Cowie et al., 2008; Joe & Daehler, 2008; Meyer & Cowie, in press). Most survive only in sparse populations (Lydeard et al., 2004; Meyer, 2006). The results indicate that *O. alliarius* and *E. rosea* would readily consume these native snails. Some native succineid species are also relatively small during the early stages of their life history, being less than 1 mm in shell length at hatching and rarely exceeding 13 mm in shell length (Brown et al., 2003; Rundell & Cowie, 2003; W. M. M., personal observations), making them vulnerable to *O. alliarius* for the first few months of their lives and to *E. rosea* for their entire lives. Achatinellids are more diverse in size. For instance, many Achatinellidae (with the exception of Achatinellinae) are widely but patchily distributed and extremely small (many < 3 mm in shell length) and are thus vulnerable to predation by both predators. Conversely, Achatinellinae, the Hawaiian tree snails, are larger. For instance, *Achatinella mustelina* are > 4 mm at birth and reach sizes greater than 21 mm in shell length (Hadfield & Mountain, 1980; Hadfield et al., 1993). Thus, while they are not likely to be consumed by *O. alliarius*, their populations have declined following the introduction of *E. rosea* (Hadfield & Mountain, 1980; Hadfield, 1986; Hadfield et al., 1993), as have similar sized Partulidae (Pacific island tree snails) following the introduction of *E. rosea* elsewhere (Clarke et al., 1984; Murray et al., 1988; Murray, 1993; Gerlach, 2001; Coote & Loève, 2003).

Although consumption rates of *O. alliarius* are much lower than those of *E. rosea*, *O. alliarius* may be having a large impact on native land snails. Populations of *O. alliarius* are more dense than those of *E. rosea* in native rain forests, notably on the islands of Hawaii and Maui, and are becoming more prevalent on other islands at higher elevations where most of the extant native snails are found (Severns, 1984, Meyer & Cowie, in press). Endangered Hawaiian tree snails are probably not impacted by *O. alliarius*, as they are too large even at birth, but much of the remaining Hawaiian land snail diversity may well be affected. Nevertheless, to ascertain the real individual and combined impacts of these predators on the land snail community as a whole and on populations of species of particular interest will require data on the population densities and size distributions of these predators as well as on the life-histories of the prey species. Unfortunately, data on population densities and life-histories for both prey and predators are few. However, investigations of these aspects of their ecology, combined with the preference and consumption rate data presented here, would permit models to be developed describing the dynamics of this system, which could help biodiversity managers protect native populations and control alien species.

Although many Pacific land-snail species are extinct, many unique species remain, representing all of the native families. Knowledge of the feeding ecology of these predators is therefore essential if natural resources managers are to design better conservation strategies targeting these remaining native species. The results of this study are relevant beyond Hawaii as both predatory snails and the introduced species used as prey species in these experiments have been widely distributed by human activities (Solem, 1964; Cowie, 2002; Coote & Loève, 2003; Barker & Efford, 2004; Cádiz & Gallardo, 2007). This may be especially pertinent for understanding the threat of these predatory snail species in the Pacific, since many native Pacific island snail faunas are composed of species belonging to many of the same families (Cowie et al., 1995; Cowie, 1996). We still have the opportunity to protect these unique lineages from extinction, but this is dependent on monitoring the presence of these predators and evaluating their impacts.

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